

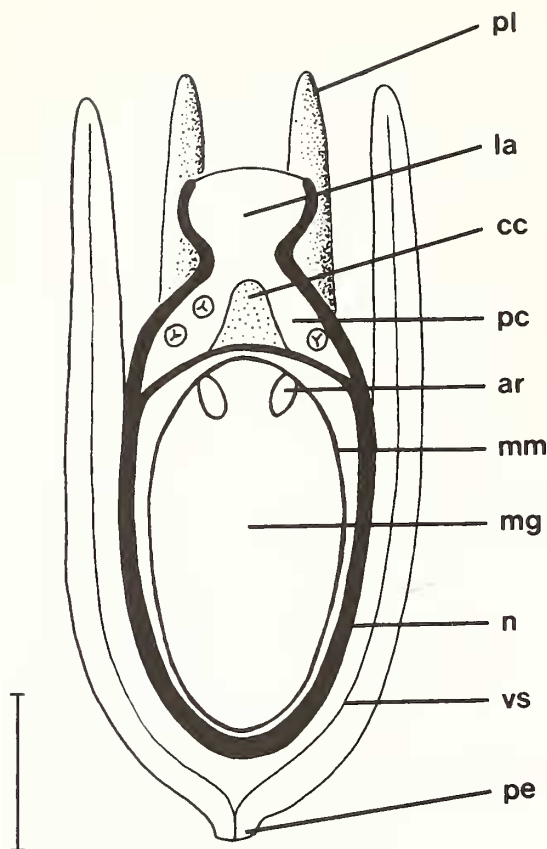
LATE DEVONIAN WINGED PREOVULES AND THEIR IMPLICATIONS FOR THE ADAPTIVE RADIATION OF EARLY SEED PLANTS

by N. P. ROWE

ABSTRACT. Winged preovules, preserved as compressions, have been recovered from the upper Famennian of Sauerland in central Germany. Preovule organization of *Warsteinia paprothii* gen. et sp. nov. includes a nucellus with distal hydrasperman lagenostome and a preintegument comprising four alate lobes. The hydrasperman organization appears to be similar to that of other well-documented Late Devonian and Early Carboniferous preovules. The alate preintegument morphology is comparable to that of permineralized preovules, such as *Lyrasperma scotica* and *Euryostoma burnense* from the upper Tournaisian of Scotland. The preintegument is differentiated into a dense inner and fibrous wing-like outer zone. The Devonian preovules represent the earliest evidence of a winged plant diaspore, and the differentiation of a preintegumentary sclerotesta and sarcotesta could be regarded tentatively as an adaptation to optimize wind-mediated dispersal. The variety of integument structures following the earliest preintegument suggests that the system of unfused, terete preintegument lobes among earliest seed plants represented an important pre-adaptation for a range of functions including protection, optimization of pollination, and dispersal.

THE appearance of the seed habit among Palaeozoic lignophytes represented one of the most important evolutionary innovations in land plants. Much has been discussed concerning the evolutionary significance of the seed habit, its pattern and timing of appearance, and its adaptive significance in conferring a number of potential selective advantages (Long 1960a, 1975; Andrews 1963; Pettitt and Beck 1968; Gillespie *et al.* 1981; Matten and Lacey 1981; Niklas 1981a, 1981b, 1983b, 1985; Tiffney 1986; Rothwell and Scheckler 1988; DiMichele *et al.* 1989; Haig and Westoby 1989; Rowe 1992a).

The earliest seed plants differed radically from plants with 'free-sporing' pteridophytic reproduction, in which sporangia were dehiscent and spores containing the haploid gametophyte generation were released directly into the environment. Under these circumstances, gametophyte growth, development of ova and spermatozooids, and syngamy (fertilization) all occurred unprotected from and unprovisioned by the parent plant sporophyte. The earliest seed plants of the late Devonian and early Carboniferous show two basic structural changes of the megasporangial complex which vastly modified sexual reproduction (Text-fig. 1). Firstly, the megasporangium no longer simply comprised a relatively uniform wall structure capable of simple dehiscence and functioning to disseminate spores, but possessed an apical opening (lagenostome) and differentiated 'pollen chamber', which functioned to trap and then direct wind-borne microspores towards the close proximity of the female gametophyte. Secondly, the megasporangium, or 'nucellus' as it is termed in seed plants, was surrounded by a layer of sterile tissue composed of four or more vascularized lobes known as the preintegument. This system of lobes is generally fused at the base, and either fused or adpressed to the surface of the nucellus inside. With the appearance of the seed habit, the development of the female gametophyte, pollination and possibly fertilization all took place within a complex structure still attached to and provisioned by the parent plant sporophyte. Generally accepted terminology refers to the unfertilized nucellus/preintegument complex as a preovule. Once fertilization has occurred and an embryo is present, the structure is referred to as a seed. The terms 'preovule' and 'preintegument' are currently used to distinguish a morphological



TEXT-FIG. 1. Longitudinal section through the middle of a generalized archetypal ovule (unfertilized seed) of an early seed plant. The haploid megagametophyte (mg) is enclosed within a single functional megaspore and surrounded by the megaspore membrane (mm). The megaspore is retained within a modified megasporangium known in seed plants as the nucellus (n). Pollination is effected via the specialized apex of the nucellus. Pollen enters the nucellar apex through the distal aperture known as the lagenostome (la) and is retained just above the female gametophyte in the pollen chamber (pc). Further development of the ovule, involving growth of the megagametophyte is believed to rupture the 'floor' of the pollen chamber and thus bring the microgametophyte into direct contact with the megagametophyte and archegonia (ar) resulting in fertilization. The central column (cc) situated in the pollen chamber is believed to enlarge and block the distal opening after fertilization. The nucellus and megagametophyte are surrounded by a ring of four or more slender pointed lobes (pl) known as the preintegument. In this diagram the section has passed along the middle of the lobes on the left and the right of the ovule and a total of six lobes would be expected. The preintegument typically has vascular strands (vs) of conducting tissue which are continuous with the parent plant via the pedicel (pe). In many of the earliest seed plants, the ovules are inserted in branched vegetative structures known as cupules (not shown). Scale bar represents 1 mm.

grade of development among seed-plants in which the sterile lobes surrounding the nucellus are not entirely fused. This differs from the arrangement generally observed in practically all seed plant ovules by the end of the Carboniferous, when the integument formed an entire structure around the apex of the nucellus, surrounding a space known as the micropyle and replacing the pollen-trapping function of the lagenostome.

Whilst there is general agreement that the seed habit represented an innovation in terms of the overall reproductive biology of land plants, there has been more uncertainty concerning the precise functional and selective significance of the principal morphological structures of the preovule. Central to this debate has been the functional rôle(s) of the preintegument, and its adaptive significance in terms of protection of the megagametophyte and embryo, and optimization of the aerodynamic properties of the preovule to enhance pollination. The traditional interpretation stresses a protective rôle of the preintegument such as a defence against dehydration, herbivory and pathogens. An alternative viewpoint, suggested by empirical biomechanical experiments, suggests that the morphology of the preintegument may have undergone modification as a result of selection for optimization of the aerodynamic properties of the megasporangium and the enhancement of pollination from wind-borne pollen (Niklas 1981a, 1983a, 1983b, 1985). Although both hypotheses may broadly contribute to an understanding of the potential ecological and evolutionary scenarios concerning the early evolution of seed plants, there is insufficient evidence to state whether one or the other functions of the preintegument represents an adaptation in the strict sense (Gould and Vrba 1982) or several pre-adaptive functions of the preintegument. An explicit determination of the adaptive significance of the preintegument is confounded by the absence of a rigorous and sufficiently inclusive phylogenetic history of early lignophytes (progymnosperms and seed plants).

It is therefore unknown whether the preintegument, initially manifested as a ring of preintegumentary lobes, appeared before or after morphological differentiation of the lagenostome (the elaborate opening of the nucellar apex) and it is probably premature to interpret the adaptive significance of the characteristic terete preintegumentary lobes characterizing many of the earliest gymnosperms as either resulting from selection for protection or optimized pollination.

The difficulty of attempting ecological and/or functional interpretations of the preintegument has been demonstrated recently by the discovery in sedimentary rocks post-dating the earliest Devonian preovules of a preovule lacking a lagenostome at the nucellar apex but possessing well-developed preintegument lobes (Galtier and Rowe 1989, 1991; Rothwell and Serbet 1992; Bateman and DiMichele 1994). Furthermore, a putatively 'ancestral' megasporangium lacking a preintegument, but equipped with a distal aperture, might, from extrapolation of the aerodynamic properties of an entirely integumented ovule, be more efficient than a partially entire or lobed preintegument. This calls into question whether the *appearance* of the preintegument could be interpreted credibly as an adaptation to aid pollination (Haig and Westoby 1989).

Many authors have discussed ecological and evolutionary scenarios based on the documented range of preovule morphologies, particularly in terms of preintegument morphology, from the upper Tournaisian and upper Viséan of Scotland. Generally speaking, this range of forms includes those with slender unfused preintegument lobes (morphologically similar to the earliest seed plant preovules) such as *Genomosperma* (Long 1959) and those with an entire integument such as *Stannostoma* (Long 1960b). This contemporaneous morphological diversity has been seen as possible evidence that early seed plants went through a period of n-selection (Arthur 1984, 1988) of low interspecific competition in empty ecospace (DiMichele *et al.* 1989) or that differing preintegument morphologies reflected a range of possibly different habitats (Niklas 1992, p. 521). Both are attractive though contrasting scenarios for explaining the morphological variation of the preintegument during the early Carboniferous, preceding the general observed trend of lobe fusion and integument-delimited micropyle towards the end of the Carboniferous.

Knowledge of the earliest seed plants has increased rapidly in the last decade as a result of intensive investigations of ancient seed plants from three principal late Devonian fossil localities in Europe and North America. These include the *Elkinsia* assemblage, Hampshire Formation in West Virginia (Gillespie *et al.* 1981; Rothwell and Scheckler 1988; Rothwell *et al.* 1989); the *Moresnetia* assemblage from the Evieux Formation in Eastern Belgium (Fairon-Demaret and Scheckler 1987) and the *Laceyia* assemblage from the Coomhoola Formation, Ballyheige in south-west Ireland (Matten *et al.* 1980a, 1980b, 1984). All contain preovules with a relatively uniform morphology, consisting of a nucellus with an apical lagenostome enveloped by a preintegument comprised of four to ten slender, terete lobes. In all three cases the preovules are inserted within cupules consisting of slightly flattened segments which are divided distally into narrower lobes. The main source of variation mostly concerns differences in size and number of preintegument lobes, and their degree of fusion with each other and the nucellus, as well as differences in symmetry, branching and organization of the sterile units comprising the cupule. At present, *Elkinsia polymorpha*, Rothwell, Scheckler and Gillespie, 1989 is probably the most completely reconstructed early seed plant, but much information is required to reconstruct most of these plants completely. Hypotheses have been put forward concerning their likely habitats in marginal, ephemeral situations with an ecological strategy as rapid colonizers of new emergent habitats. These scenarios intuitively embrace the selective advantages of pollination, protection and dispersal resulting from acquisition of the seed habit.

Although the fossil record of the earliest seed plants is well documented from upper Famennian clastic sequences of Euramerica, marine sediments dominate many areas directly succeeding the Devonian/Carboniferous boundary. It is only by the upper Tournaisian that plant assemblages are known demonstrating diverse anatomically preserved spermatophyte fertile structures, and which reflect morphological radiation on a large scale with significant structural and functional divergences from the 'ancestral gymnosperms' of the late Famennian (Long 1960a, 1960b, 1969, 1975, 1977a, 1977b). Many of the putative seed plant findings from uppermost Devonian, and lower

and middle Tournaisian sedimentary rocks are known only from marine or highly allocthonous deposits where seed plant reproductive organs are uncommon and/or poorly preserved. Recent findings from the middle Tournaisian 'Lydiennes' deposits of southern France exemplify this situation with a single specimen of *Coumiasperma remyii* recorded (Galtier and Rowe 1989, 1991). More articulated compression material from a lithological variation of the 'Lydiennes' at La Serre, southern France, has yielded a variety of putative seed plant, rachises, foliage and cupules but lacking unequivocal *in situ* preovules (Rowe and Galtier 1990). While the morphology of some of these cupule compressions may be consistent with those seen in late Famennian gymnosperms others are reminiscent of more derived, compact, cupules from the Lower Carboniferous of Scotland. If the interpretation of the compression material from La Serre is correct, it provides compelling evidence that significant diversification of cupule morphology had occurred by the mid Tournaisian.

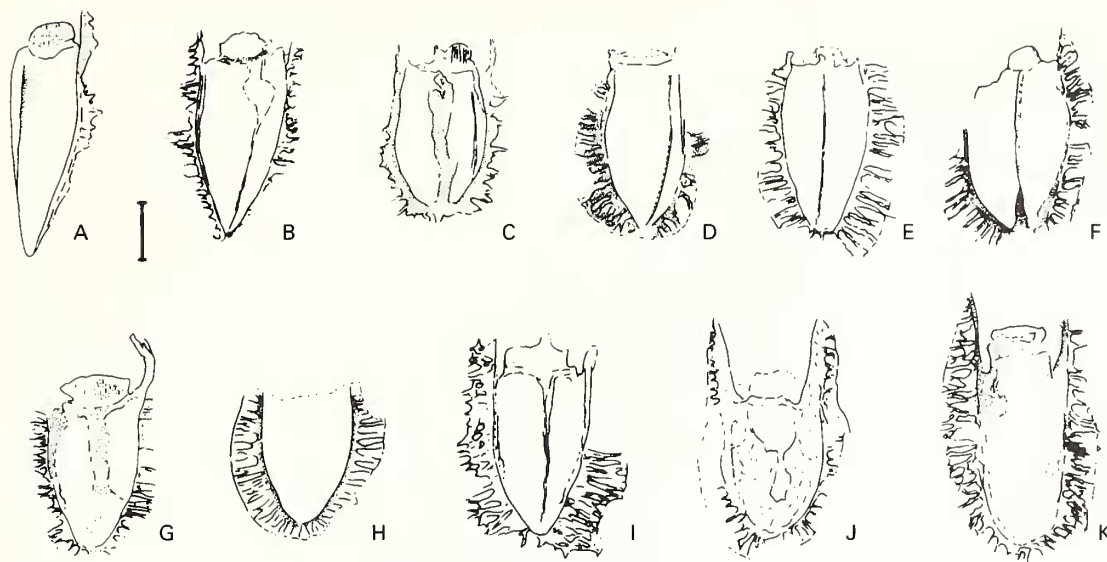
The object of this paper is to describe and discuss some preovules with winged preintegumentary lobes from the upper Famennian of central Germany. Although, only occurring as isolated units, they provide evidence of significant diversification of preovule morphology prior to the end of the Devonian and the wide morphological diversity observed in the late Tournaisian.

LOCALITY INFORMATION

The Hangenberg Sandstein at Oese, central Germany is situated in an abandoned roadside quarry beside the B7 road, between Menden and Hemer, approximately 12 km south of the river Ruhr (Higgs and Streel 1984; Keupp and Kompa 1984). At the base of the section, Wocklum limestone is succeeded by a narrow bed of Hangenberg Schiefer which is typical of the Upper Devonian lithofacies of the Remscheid-Altena anticline in the Rheinisches Schiefergebirge (= Rheinisch Slate Mountains) of central Germany (Higgs and Streel 1984). At Oese, a local variation of the Hangenberg Schiefer is present as a series of coarser sandstones with a south-westerly provenance and interpreted as an off-shore deposit in a high energy depositional environment in the proximity of off-shore reefs (Keupp and Kompa 1984). At Oese, approximately 12 m of sandstones are succeeded by a thin band of Hangenberg limestone which marks the Devonian/Carboniferous boundary (Luppold *et al.* 1994). Beds 2–4 m below the D/C boundary in the Hangenberg Sandstein have been dated stratigraphically on the basis of conodont faunas giving a lower *Protognathodus* Zone, and meiospore assemblages giving a LN biozone in the uppermost Famennian. Above the boundary beds, Tournaisian sedimentary rocks are dominated in the region of the Rheinisch Slate Mountains by black marine shales (Alaunschiefer) and radiolarian cherts which are also exposed in a small subsidiary cutting adjoining the main quarry at Oese. Although permineralized plants have been identified from these sedimentary rocks and from a nearby locality at Oberrödinghausen (Rowe 1992b; Rowe *et al.* 1993), plant material has not been recovered from the Alaunschiefer at Oese.

Plant fossil material is found throughout the exposed sequence of Hangenberg Sandstein. The sandstone consists of at least eight to twelve beds up to 1 m thick consisting of upward fining sequences from very coarse, micaceous, sandstones to narrow layers of fine shale. The plant macrofossils may be divided into four broad categories, which appear to be facies controlled and comprise: (1) poorly preserved, flattened compressions of axes (sometimes orientated) up to 0.15 m long, recovered from coarse micaceous levels throughout the section; (2) three-dimensional moulds and casts of axes most usually confined to the coarser facies; (3) dark red to light orange, petrified, (probably limonitized) axes up to 0.35 m long showing anatomy and found throughout coarse sandstone and fine shale bands; (4) highly fragmentary, densely deposited, plant meso-debris, occurring in thin bands (10–40 mm) of laterally discontinuous, localized shales at the top of several upward fining sequences of coarse sandstone.

The preovules come predominantly from the type (4) facies association. They are similar in size to much of the rest of the indeterminable plant meso-debris and are the most common identifiable plant organs. The remainder of the meso-debris consists of indeterminable axes, rarely more than



TEXT-FIG. 2. A–K, preservational variants of *Warsteinia paprothii*. The ovule compressions vary considerably in the appearance of the nucellar apical region, in the appearance and integrity of the outer preintegument lobe tissue and in the variable positioning and appearance of medianly positioned preintegument lobes. A, V.64114a; B, V.64115a; C, V.64116a; D, V.64117a(1); E, V.64118a(1); F, V.64119; G, V.64118a(2); H, V.64120; I, V.64118a(3); J, V.641121a; K, V.64113a. Scale bar represents 1 mm.

1–2 × 10–20 mm, megaspores and fragments of highly divided foliage and broader spatulate pinnules. Exceptions to this broad category include a branched non-cupulate ovulate structure and rare ‘leaf’ fragments with an open dichotomous nervation which are comparable to compression foliage of *Archaeopteris*. Small fragments of fossil charcoal (pyrofusain) are also consistently observed in this facies.

Plant material from the coarser facies type consists of anatomically preserved axes of cladoxylaleans and protostelic lignophytes reaching up to 0.35 m long. Also common are compressions and casts of petiolate, bifurcate rachises, occasionally with pinnules in attachment, and compressions and casts of leafy or decorticated lycopsid axes, microphylls and sporophylls.

METHODS AND MATERIALS

Preovules are preserved as carbonaceous compressions throughout the exposed section of the Hangenberg Sandstein, predominantly from the finer-grained horizons and occasionally from the coarser, highly micaceous sandstones. Most specimens show evidence of organic material visible as black vitrinite or dark to light brown material resembling oxidized cuticle. Oblique, semi-polarized light and SEM observation of the finest impression surfaces occasionally yielded limited data on cell size and alignment. Uncovering the material with fine needles was successful in revealing substantial parts of the preovule compression but smaller-scale uncovering was difficult because of organic material adhering to the large sediment grains and mica.

Interpretation of small-scale three-dimensional features involved critical observation of the course of the surfaces exposed by the fracture plane through the compression fossil. Embedding followed by sectioning with a diamond wafering blade did not yield informative sections. The three dimensional arrangement of the preovule was made possible by careful consideration of both parts and counterparts of a number of key specimens. Macrophotography (up to × 16) was carried out on a Zeiss Tassovar with intense, polarized, fibre optic light source. Higher magnification was

achieved by placing the specimen directly on the stage of a Nikon compound microscope fitted with incident cross-polarized lighting and Nikon BD Plan objective lenses. This technique provided high magnification micrographs up to $\times 230$, rivalling those obtained from cellulose acetate surface peels but leaving the compression intact.

All specimens are deposited in the Department of Palaeontology, The Natural History Museum, London, specimen numbers V.64113 to V.64121.

DESCRIPTION

More than 160 isolated preovules were examined. There is a high degree of variation in shape, overall size and presence or absence of main features. Study was confined to well-preserved specimens showing combinations of at least two of the following structures: (1) a preintegument, (2) a nucellus, (3) apical elaboration of the nucellus into a lagenostome. Based on these criteria, approximately 20 specimens showing well-preserved, key characters were selected for study. Many other specimens from the assemblage lacked one or more of these structures and therefore could not be interpreted definitely as preovules.

Preovule morphology

The most complete preovule compressions have overall dimensions varying from 3.3–4.7 mm long and 2.3–3.0 mm wide (Text-fig. 2). The preovules consist of a central oval nucellar region, a distal extension of this into an apical lagenostome, and a preintegument. The appearance of all three of these structures is strongly dependant on the three-dimensional extent of the compression, the degree of sediment accretion around the lagenostome and preintegument lobes, and the passage and direction of the plane of fracture passing through or around the compression/matrix structure when the rock was split.

The nucellar region is pointed proximally and broadens to 1.1–1.4 mm just above the mid-level of the preovule (Pl. 1, figs 1–2). Near to the apex of the preovule, the nucellus is contracted slightly (Pl. 2, figs 1–2) and this level is interpreted as the distal limit of the pollen chamber. In some specimens the structure interpreted as the lagenostome is visible as an extension of the nucellar apex, about 0.5 mm wide and 0.5 mm long. The original ‘tube-like’ nature of the lagenostome is visible in some specimens where sediment has entered the opening and lagenostome has retained a three-dimensional structure as a minute cast, in contrast to the rest of the preovule which became flattened (Pl. 2, fig. 2).

The appearance of the preintegument is the most variable feature as a result of a variety of presumed taphonomic processes. Well-preserved, laterally orientated compressions often show evidence of a preintegument lobe at each side of the nucellar region (Pl. 1, fig. 1; Pl. 2, fig. 3). Each

EXPLANATION OF PLATE 1

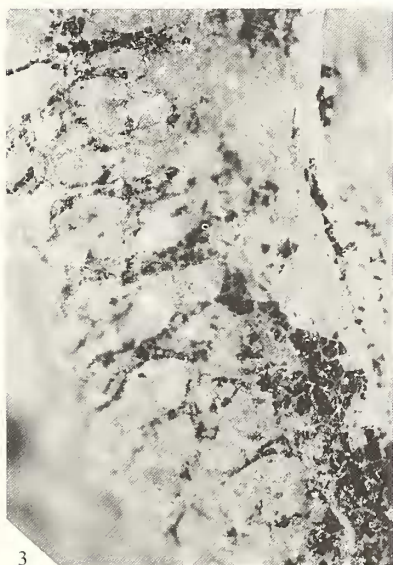
Figs 1–5. *Warsteinia paprothii* gen. et sp. nov.; Oese; Upper Devonian. 1, V.64113a, holotype (part); carbonaceous compression of entire winged ovule showing evidence of two prominent alate preintegument lobes to the left and right and a lagenostome at the apex of the nucellus; $\times 25$. 2, V.64114a; ovule with slender nucellar region and highly abraded alate preintegument lobes; a common preservational variant at the locality, in which alate ovules resemble ovules with slender preintegument lobes; evidence of three preintegument lobes is visible on the part of this specimen; the lagenostome is well preserved and sediment filled; $\times 25$. 3, enlargement of fig. 1; fimbriate appearance of the alate preintegument lobe compression consisting of an inner dense region (lower right) and an outer region of ‘radiating strands’; $\times 60$. 4, enlargement of fig. 1; preintegument lobe showing continuity of less-dense organic compression material between ‘radiating strands’; $\times 60$. 5, V.64117a(2), preintegument lobe of organically well-preserved ovule showing continuity between radiating strands and integrity of the outer margin; $\times 50$.



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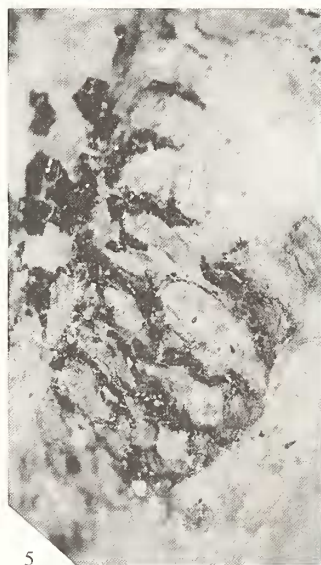
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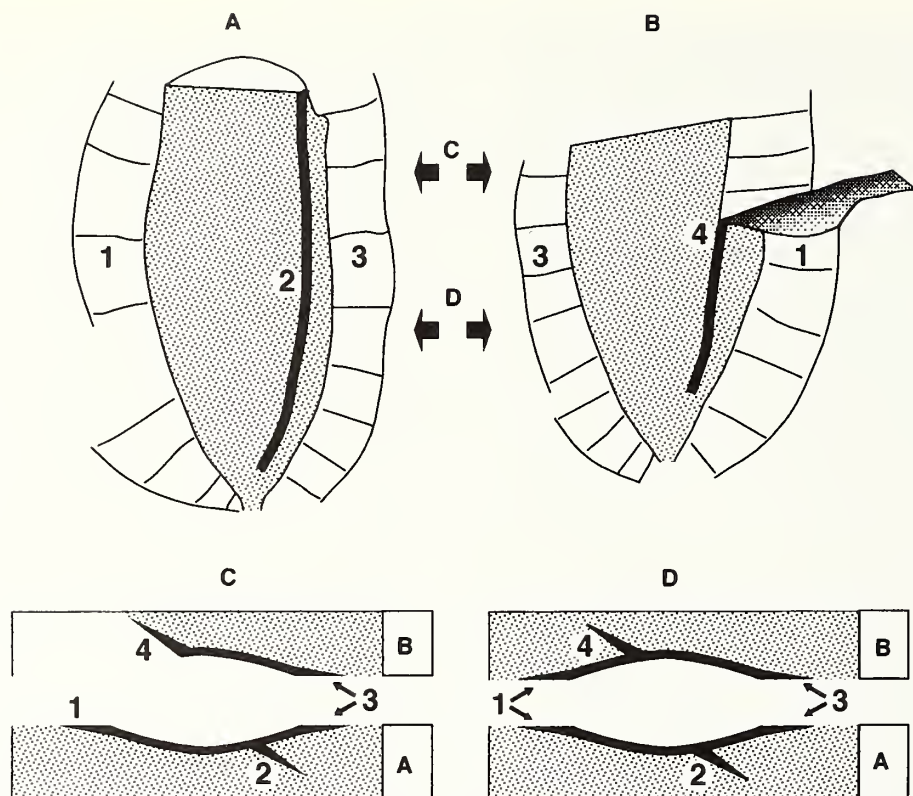
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TEXT-FIG. 3. Interpretive diagram of three-dimensional disposition of preintegument lobes from part and counterpart of single specimen of *Warsteinia paprothii*, V.64117(1), (see also Pl. 3). A, V.64117a(1); ovule part with evidence of preintegument lobes (1–3); the central lobe (2) is not exposed by the plane of fracture but is visible as a longitudinally aligned groove filled with organic material. B, V.64117b(1), counterpart of ovule also showing parts of lobes 1 and 3 in addition to the medianly positioned lobe 4; the plane of fracture has removed the sediment separating the distal parts of lobes 1 and 4 to expose the compression surface of lobe 4. C–D, idealized section through distal (C) and proximal parts (D) of part/counterpart complex.

lobe consists of two discrete zones: a dense inner organic layer, and an outer network of interconnected but generally radially aligned strands (Pl. 1, figs 3–5). These are referred to as the sclerotesta and sarcotesta respectively. Each preintegument lobe is 0.65–0.77 mm wide at its broadest point just below the mid-level of the preovule, and tapers gradually to the apex about 0.6–0.8 mm above the lagenostome. Around the base of the preovule the lobe is only slightly narrower than at the widest part. Differentiation of the challazal region is unclear but several specimens (e.g. Pl. 3, figs 1–2) indicate a slender proximal extension of the nucellar region resembling part of a stalk.

Preintegument lobes are either fused or consistently adpressed to the nucellus for two-thirds of the total preovule length, and appear to separate from the nucellus just below the level of the lagenostome and the inferred position of the pollen chamber (Pl. 1, figs 1–2). The darker sclerotesta consists of much denser organic material, which is comprised of longitudinally aligned strands, or cellular elements (Pl. 2, fig. 4) which taper distally but remain conspicuous above and below the level of contact of the preintegument to the nucellus (Pl. 1, fig. 1).

The sarcotesta occupies the greater part of each preintegument lobe and comprises less dense, generally radially aligned fibre-like tissue, which forms an interconnecting network (Pl. 1, figs 3–5).

This is delimited on the outside of the preintegument lobe, in exceptionally preserved specimens, by a peripheral continuation of the fibre-like network forming the outer perimeter of each 'wing'. This has a highly variable appearance (Pl. 1, figs 3–5), according to preservational differences between specimens, and varies from a simple fimbriate appearance (Pl. 1, fig. 3), to one in which continuous organic material is visible between fibrils (Pl. 1, fig. 4), to one in which a continuous outer perimeter is organically preserved (Pl. 1, fig. 5). Individual strands are 15–40 μm wide and anastomose, undergoing from two to four divisions to the outside of the sarcotesta. They are interconnected laterally by less dense organic material, which apparently integrates in density between adjacent strands.

Organization of the preintegument

Few specimens show direct evidence of the number of preintegumentary lobes. Evidence of more than two lateral preintegument lobes is variable, and depends on the degree of three dimensional preservation and orientation of the preovule in the matrix. Highly flattened specimens may show one or two darker carbonaceous longitudinal bands along the mid-region of the nucellus (Text-fig. 2). More than two lateral preintegument lobes are seen most clearly among the rarer three-dimensionally preserved preovules where they are visible as prominent longitudinal grooves (Pl. 3, figs 1–4; Text-fig. 3). Occasionally the plane of fracture follows one or more of these grooves to expose the planar surface of a third preintegument lobe beneath (Pl. 3, fig. 4, arrow; Text-fig. 3B, lobe 4).

Text-figure 3 depicts part and counterpart of a three-dimensionally preserved preovule in which substantial sediment accretion occurred between preintegument lobes during burial of the seed and prior to compression (Pl. 3, figs 1–2). Both part and counterpart show a preintegument lobe visible as a longitudinal groove along the mid-region of the nucellus, in addition to the pair of lobes at each side (Text-fig. 3A–B). The preintegument lobes are numbered 1–4 in an anti-clockwise direction when part and counterpart are depicted together (Text-fig. 3C–D). The plane of fracture has exposed all of lobes 1 and 3 but has only exposed the distal part of lobe 4, which is visible proximally as a longitudinal groove.

The new structures are interpreted as seed plant preovules, as a result of the identification of a preintegument divided into lobes surrounding a nucellus with a differentiated apical lagenostome. The basic organization of this morphology is consistent with that of other well-documented preovules from the upper Famennian to the Upper Carboniferous. The organization of the sclerotesta and sarcotesta suggests that the former is entire and fused, or adnate to the nucellus to just below the base of the lagenostome. It is not possible to determine the precise extent of fusion between preintegument lobes. The density of the organic material remaining around the long axis of each preintegument lobe and around the nucellus suggests that the sclerotesta is continuous or fused around the nucellus. In each preintegument lobe, the sarcotesta is differentiated into a winged extension. Above the apical part of the nucellus the preintegument lobes arch out slightly above the level of fusion of the preintegument with the nucellus. Nothing is currently known about the mode of attachment of the preovule or whether the preovules were cupulate.

SYSTEMATIC PALAEOONTOLOGY

Division SPERMATOPHYTA (following Rothwell and Serbet 1994)

Order LYGINOPTERIDALES? (*sensu* Barnard and Long 1975)

Family unknown

Genus WARSTEINIA gen. nov.

Derivation of name. Warstein, a town in Sauerland, Germany.

Type species. *Warsteinia paprothii* sp. nov. from the upper Famennian, Oese, Sauerland, Germany.

Diagnosis. Compressions of isolated preovules with four winged preintegumentary lobes. Preovules 3.3–4.7 mm long and 2.3–3.0 mm wide. Nucellar region oval, 1.1–1.4 mm wide in broadest part at mid-level of preovule, pointed proximally and differentiated distally into apical lagenostome, 0.5 by 0.5 mm, with angular proximal differentiation of presumed pollen chamber. Preintegument lobes adnate or fused to nucellus to just below pollen chamber, comprising an inner dense sclerotesta composed of longitudinally aligned elements and an outer sarcotesta comprised of perpendicularly aligned anastomosing fibrous strands.

Warsteinia paprothii gen. et sp. nov.

Plates 1–3; Text-figures 2–4

Derivation of name. In honour of Dr Eva Paproth.

Holotype. V.64113a–b; roadside quarry on the B7 road at Oese between Menden and Hemer, Sauerland, central Germany; Hangenberg Sandstein, Upper Devonian, upper Famennian, LL–LN miospore biozone.

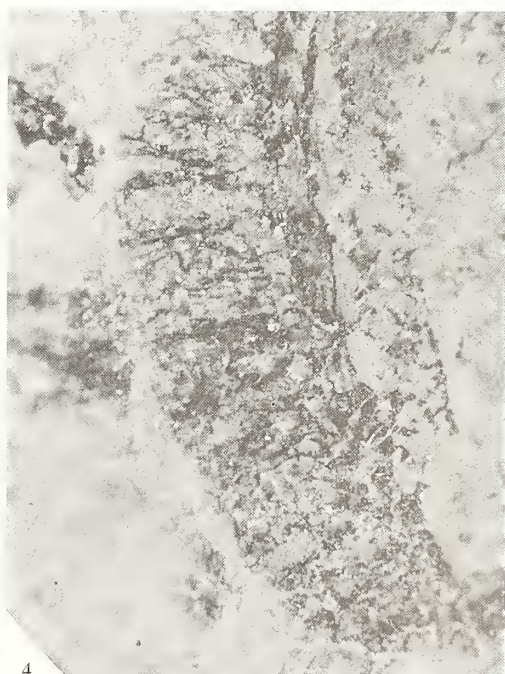
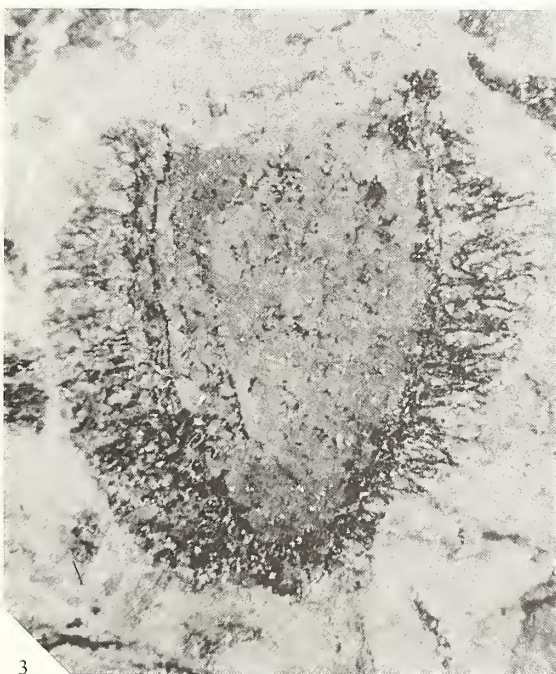
Diagnosis. As for genus. This is the only recognized species.

COMPARISONS WITH OTHER DEVONIAN AND EARLY CARBONIFEROUS PREOVULES

Comparisons of other late Famennian preovules indicate that, apart from differences in overall size, and number and degree of fusion of preintegument lobes, there is little major difference in morphology (Fairon-Demaret and Scheckler 1987; Rothwell and Scheckler 1988; Rothwell *et al.* 1989). The best known Famennian preovules (*Elkinsia polymorpha* Rothwell, Scheckler and Gillespie, 1989, *Moresnetia zaleskyi* Stockmans, 1948 and *Kerryia mattenii* Rothwell and Wight, 1989) all consist of a preintegument divided into four or five, or eight to ten lobes surrounding a nucellus differentiated apically into a pollen chamber and lagenostome. Differences in preovule morphology mainly concern the number of preintegument lobes and the degree of fusion or adpression with each other and the nucellus. Preintegument lobes are fused to the nucellus for one-third and one-half the length in *Elkinsia* and ovules of *Kerryia*, respectively, but only at the base in *Moresnetia*. This appears to be the most marked difference separating these preovules. Other differences include the relative size and shape of the pollen chamber and lagenostome, and the overall size and shape of the preovule. However, these characters are difficult to quantify between genera due to presumed changes associated with ontogeny of the gametophyte, pollination, fertilization, and sporophyte development. The main characters distinguishing the German

EXPLANATION OF PLATE 2

Figs 1–4. *Warsteinia paprothii* gen. et sp. nov.; Oese; Upper Devonian. 1, V.64113a, holotype; enlargement of Plate 1, fig. 1, showing continuity of preintegument lobe with nucellar region to just below the lagenostome, and the angular differentiation between the top of the nucellus (probable pollen chamber) and the lagenostome (arrow); $\times 42$. 2, V.64114a; enlargement of Plate 1, fig. 2, showing similar differentiation at the apex of the nucellus as seen in Plate 2, fig. 1; the remains of the highly abraded alate lobe are just discernible (arrow a), while a linear groove clearly marks the position of a third preintegument lobe in the median part of the nucellar region (arrow b); $\times 47$. 3–4, V.64120. 3, proximal part of an ovule exposed by the plane of fracture which has removed the apical part of the nucellus and lagenostome (a common preservational variant); $\times 25$. 4, enlargement of fig. 3 showing evidence of longitudinally orientated carbonaceous material (inner preintegument) continuous with perpendicularly orientated alate part of the outer preintegument; $\times 44$.

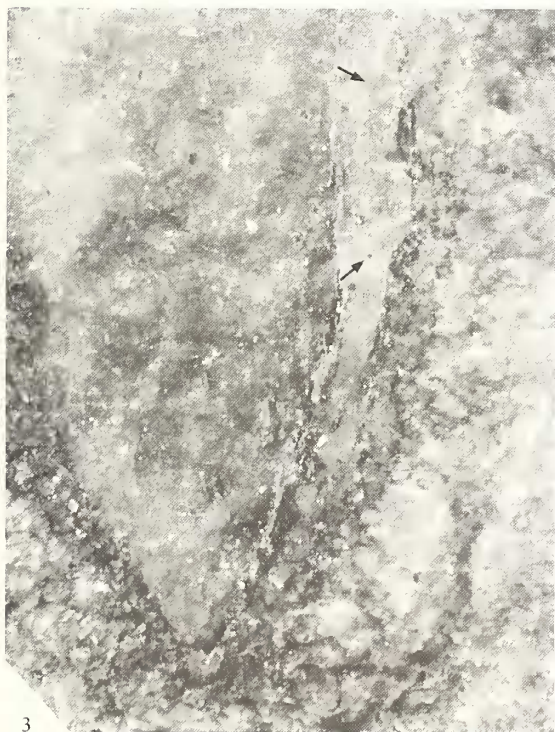


preovules from *Elkinsia*, *Moresnetia* and *Kerryia* are the winged preintegument lobes differentiated into sclerotesta and sarcotesta. In surface view, each winged lobe occupies up to 60 per cent. of the area of the compressed nucellar surface. The preintegument lobes of the new seeds are over twice the width calculated from published accounts of *Moresnetia* and *Kerryia* (Fairon-Demaret and Scheckler 1987; Rothwell *et al.* 1989). In addition to this, there is no evidence in any of the genera mentioned above of a preintegument lobe organization more complex than a vascular strand positioned centrally in a simple, terete, distally tapered lobe (Text-fig. 1).

In *Archaeosperma arnoldii* Pettitt and Beck, 1968 the preintegument lobes are fused up to the level of the pollen chamber area, above which each extends as a small terete tip. The surface of the preintegument of *Archaeosperma* possesses spine-like emergences which can appear quite dense in laterally orientated preovule compressions. These appear similar to poorly preserved preintegument lobes of *Warsteinia* in cases when the outer margin of the sarcotesta is not visible and the thinner organic material grading between the radially orientated strands is not preserved (Pl. 1, figs 2–3). *Xenotheca devonica* Arber and Goode, 1915 from the upper Famennian of north Devon is one of the least known cupulate preovules (see also Rogers 1926). More recent reports of these structures (Fairon-Demaret and Scheckler 1987; Rothwell and Scheckler 1988) indicated that the terete, apparently slightly fused preintegument lobe organization of the preovules, and the morphology of the cupules, is similar to *Elkinsia* and *Moresnetia*. One of the least-well understood putative preovules from the Upper Devonian is *Spermolithus devonicus* Chaloner, Hill and Lacey, 1977 from the 'Old Quarry' at Kiltorcan in southern Ireland. The outline and shape of these seed-like structures were compared with compressions of platyspermic seeds assigned to the form genus *Samaropsis* and the anatomically preserved *Lyrasperma scotica* (Calder) Long, 1960a from the Lower Carboniferous of Scotland (Calder 1938; Long 1960a). Morphological evidence was considered sufficient to interpret the Kiltorcan structures as platyspermic, bilaterally symmetrical gymnospermous preovules. There is apparently no evidence of an elaborated nucellar apex in the central, apical position of *Spermolithus* which would be expected if the material was of the same structural complexity as *Lyrasperma* (Stewart 1983, p. 236) or indeed any other preovule with a hydrasperman modification of the nucellar apex. The main question is whether both an integument and a nucellus are present in the material. Chaloner *et al.* (1977) interpreted a central, oval structure in the centre of each structure as a megaspore. The boundary between this and the outer surrounding structure is relatively clear, but outside the central oval area there is no consistent differentiation suggesting the presence of both an integument and a megasporangium/nucellus. It is therefore possible that the material represents a megaspore within a dehiscent megasporangium, as suggested perhaps by the irregular opening or split at the apex of the structure. This interpretation is perhaps more likely in the absence of convincing evidence of an integument and nucellus, or a structure resembling an elaborated nucellar apex or lagenostome. The preovules from Oese clearly differ from *Spermolithus* in possessing features consistent with a hydrasperman preovule morphology. In addition, the platyspermic appearance of certain preovule compressions

EXPLANATION OF PLATE 3

Figs 1–4, *Warsteinia paprothii* gen. et sp. nov.; Oese; Upper Devonian; part, V.64117a(1) and counterpart, V.64117b(1) of single ovule showing preservational organization of four preintegument lobes (see also Text-fig. 3). 1, V.64117a(1), showing evidence of three preintegument lobes (arrows), lobe 1 at left, lobe 3 at right and lobe 2 towards the right of the nucellar region; $\times 28$. 2, V.64117b(1) counterpart, showing evidence of preintegument lobes 1 and 3, to the right and left of the specimen; a fourth preintegument lobe (lobe 4) is visible towards the right of the nucellar region; $\times 44$. 3, enlargement of fig. 1, showing carbonaceous material of lobe 2 disappearing into the matrix; lobe 2 is separated from lobe 3 by a linear sliver of fine matrix (arrows); note the attenuated proximal outline of the ovule suggestive of differentiation into a narrow basal stalk; $\times 28$. 4, enlargement of fig. 2, showing where the plane of fracture has exposed the distal surface of preintegument lobe 4 (arrow) by passing through the sliver of sediment separating lobes 1 and 4; $\times 44$.



may be belied by the effects of compression. This is clearly the case with *Warsteinia* in which four preintegument lobes are present with a probable rotational symmetry (Rothwell 1986) of 90°.

Well-documented preovules from the Lower Carboniferous are known mostly from strata no older than the CM biozone of the upper Tournaisian. Many anatomically preserved, putative seed plants from earlier in the Tournaisian are found only in marine black shales and cherts. These sedimentary rocks yield mostly vegetative stems, petioles and rachises, which were probably rafted into the marine depositional environment, and contain very few reproductive organs. As a result, very few seed or cupulate organs are known from this period so that much of our knowledge of the diversity of early seed plants in the earliest Carboniferous, is limited to vegetative axes and leaves.

One single example of an anatomically preserved preovule is known from the middle Tournaisian 'Lydiennes' formation of the Montagne Noire in southern France (Galtier and Rowe 1989, 1991). The structure consists of eight relatively massive preintegument lobes surrounding the nucellus. The apex of the nucellus lacks a pollen chamber and consists only of a solid parenchymatous nucellar beak, in spite of the fact that preovule ontogeny had proceeded sufficiently to develop cellular endosporic gametophyte tissue. The pattern observed in the compressed preintegument lobes of *Warsteinia* could conceivably represent, in terms of size and width to the nucellus, a compressed version of the permineralized preintegument lobes of *Coumiasperma*. However, the aerenchymatous tissue and position of the vascular trace in *Coumiasperma* is not consistent with the arrangement of inner dense and outer strand-like organic material observed in *Warsteinia*. Firstly, in *Coumiasperma* the vascular strand is positioned centrally in the preintegument lobe. Secondly, the tissue of the preintegument lobe is aerenchymatous and, although some of the cellular components are aligned perpendicularly, there is no evidence of well-defined fibrous elements.

More than 25 species from 15 genera of permineralized preovule are known from the upper Tournaisian to upper Viséan of Scotland (Rothwell 1986). Apart from the record of *Coumiasperma* from the middle Tournaisian of France, the assemblages from Scotland have, up to now, represented the earliest evidence of a wide-scale diversification in preovule morphology, which is observed mostly in terms of preintegument structure with differences in size and shape of the lagenostome and pollen chamber relative to the nucellus.

Apart from size, structural variation of the preintegument may be characterized broadly among Early Carboniferous preovules in terms of: (1) number and symmetry of preintegument lobes; (2) extent of fusion or adpression of the preintegument to the nucellus; (3) position of vascular strand in each preintegumentary lobe; (4) presence/absence of hairs, spines; and (5) lobe/ridge differentiated into endotesta (sclerotesta) and sarcotesta.

The well-documented preovules from the Famennian show variations in some or all of characters (1) to (5). Some of the preovules from the CM biozone and younger strata, such as *Hydrasperma tenuis* Long, 1961, differ so little from the 'ancestral' preovule morphology described for *Elkinsia*, *Moresnetia* and *Kerryia*, that as isolated units they cannot be distinguished from the older preovules (Matten *et al.* 1980a; Rothwell and Wight 1989).

The fifth main type of divergence is the appearance of a 'winged' preintegument as shown by *Lyrasperma scotica* and *Euryostoma burnense* (Long) Long, 1975. Both preovules possess a preintegument differentiated into sclerotesta and sarcotesta, the latter forming extended 'wings' or 'keels'. The inner integument is entire around the preovule proximally, but more distally both endotesta and wing-like sarcotesta are individual free winged lobes (Calder 1938; Long 1960a, 1969). It is this organization which is most comparable to that observed in the new Famennian preovules from Germany. Winged lobes are most developed in *Lyrasperma*. In *E. angulare* Long, 1969, there is a broadly similar differentiation of inner and outer preintegument tissue but the lobes are narrower (Calder 1938; Long 1960a). In *E. burnense* the inner sclerotesta consists of dense, longitudinally aligned fibrous tissue material completely surrounding the nucellus, which also partially envelops the vascular bundle of each winged lobe (Long 1969). Both the sclerotesta and vascular bundles are positioned close to the inner surface of the preintegument in contact with the nucellus. In *E. burnense* the tissue outside the sclerotesta is described as being comprised of alternating bands or plates of thick-walled cells with softer tissue which seemed to have decayed.

In *Lyrasperma* a similar but not identical organization of tissue types is observed in which the vascular bundles of each preintegument lobe are partially enveloped by radially aligned flanges of the inner sclerotesta. The wing-like extensions forming each preintegument lobe are comprised of transversely aligned, multicellular strands apparently separated by intercellular spaces (Calder 1938; Long 1960a).

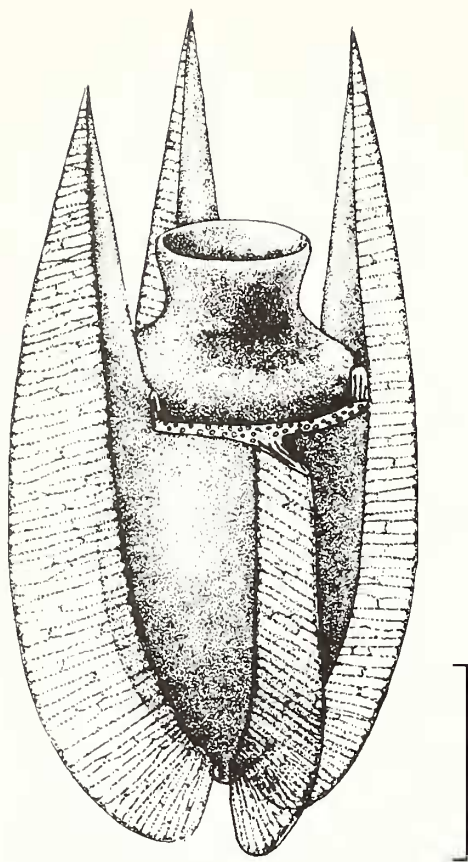
Warsteinia paprothii is smaller than all three preovules discussed above by factors of four to eight. Because of differences in preservation it is difficult to make detailed comparisons. There is a strong implication that the winged preintegument organization comprises a dense inner tissue possibly containing the preintegument vascular strand (Text-fig. 3) and an outer wing-like tissue comprised of resistant fibrous tissues alternating with thinner material.

DISCUSSION

The preovules from Germany (Text-fig. 4) demonstrate that significant divergence in preintegument morphology had occurred among seed plants with hydrasperman reproduction before the end of the Devonian. This obviously predates the late Tournaisian, CM biozone divergence, previously reported as marking the timing of a major diversification among seed plants (Andrews 1963; DiMichele *et al.* 1989). The appearance of a differentiated sclerotesta and wing-like sarcotesta by the late Devonian represents a relatively high level of divergence compared with the variability observed among previously known, well-documented Devonian preovules.

Despite the increase of morphological information on early seed plants, much uncertainty still exists in elucidating functional and life history processes. Equally difficult have been attempts to interpret possible adaptive rôle(s) of the key morphological structures of the seed as well as determining which selective forces were operating on the earliest seed plants (Niklas 1983a, 1985; Haig and Westoby 1989; Rothwell and Wight 1989). The ring of simple terete preintegumentary lobes observed in the earliest seed plants possibly represents a structure pre-adapted for a range of possible functions following modification (Gould and Vrba 1982). Rothwell and Scheckler (1988) demonstrated evidence of developmental post-pollination shifts in preintegument arrangement around the nucellus in *Elkinsia*. It is unknown exactly to what extent this arrangement afforded protection to the nucellus, as the lobes are unfused for most of their length. Also this development was not observed in *Moresnetia* in which preintegument lobes are described as less-fused laterally. It is possible that among the earliest seed plants, preintegumentary lobes provided little or no protection to the megagametophyte and embryo. If this is the case the appearance of preintegument lobes may have been initially non-adaptive but pre-adapted for a number of functions following the relevant structural modifications: fusion (protection); centripetal differentiation into wings (air mediated dispersal); development of air spaces (water mediated dispersal); or entire fusion (aerodynamic optimization for pollination). One of the most intriguing discussions concerning the early evolution of the seed habit concerns the ecological and evolutionary processes characterizing the morphogenesis of the preintegument and their consequences on pollination, protection and dispersal.

Recent studies on the reproduction of early seed plants have focused on the pollination process and have determined the precise functioning of the lagenostome, pollen chamber, central column and pollen chamber floor during pre- and post-pollination phases (Rothwell and Scheckler 1988; Rothwell and Wight 1989; Rothwell and Serbet 1992). There is, however, far more uncertainty concerning the functional rôle of the preintegument prior to the evolution of an entire integument, whether it acted (1) as protection against desiccation, herbivory and microbial activity or (2) to maximize pollination (Niklas 1981a, 1981b, 1983a, 1983b, 1985) (i.e. aerodynamic optimization of the preovule for the deposition of pollen at the nucellar apex). As the individual preovule (nucellus and preintegument) represented the abscised diaspore or unit of dispersal, a third functional rôle for the preintegument among early seed plants may have included one of dispersal. There is no direct evidence that any of the cupulate structures characterizing early seed plants before the late Carboniferous functioned as part of the diaspore unit and that modification of the early seed plant



TEXT-FIG. 4. Reconstruction of *Warsteinia paprothii* with prominent winged preintegument lobes adpressed or fused to the nucellus to just below the differentiation of the lagenostome. The inner preintegument layer is reconstructed here as if entire around the nucellus although this is equivocal. The cut-away portion of the preintegument indicates the orientation of the linearly and perpendicularly aligned organic material of the inner and outer preintegument layers. Scale bar represents 1 mm.

diaspore for dispersal would have required modification of the seed itself. Rothwell and Scheckler (1988) described attached cupules bearing only the proximal parts of seed stalks which suggests direct evidence of seed abscission/dispersal. However, they also reported isolated cupules bearing seeds and the possibility exists that cupule/seed complexes might have functioned as diaspores in *Elkinsia*, or reflect a tendency towards senescence, withering and fragmentation at maturity. If the German preovules are interpreted correctly, they show a number of similarities with winged diaspore features of more recent fossils and many extant diaspores demonstrated by a fibrous network surrounded by thin membranous material (Ridley 1930; van der Pijl 1969; Augsburger 1986; Tiffney 1986).

Recent studies have shown that the fall velocities and potential dispersal distances of extant diaspores are dependant on 'wing loading' (expressed as the weight divided by the surface area of the diaspore) in addition to the aerodynamic movement of the diaspore during descent, which is governed primarily by the shape of the object (Green 1980; Augsburger 1986). Diaspores with similar wing-loads may differ significantly in their descent velocity on account of their variable aerodynamic movement. Numerous studies have identified the aerodynamic characteristics of modern plant diaspores, with some authors grouping similar aerodynamic movements. However, without the appropriate data concerning the relative densities and accurate three dimensional reconstruction, it is difficult to estimate what sort of aerodynamic movement these seeds would demonstrate. For example, all of the familiar autorotating diaspores examined by Augsburger (1986) possess only one wing, with the heaviest mass concentrated either in the centre (rolling autogyros) or at one end (autogyro). Neither of these broad morphologies fits that of the Devonian

preovule described here, which resembles more, in shape but not in overall size, a fruit described as a 'tumbler' (Augsburger 1986) which have been demonstrated to descend, as implied by the name, in a more irregular fashion.

The new winged seed, and others such as *Lyrasperma*, may show evidence of a decreased 'wing-loading' compared with earlier and contemporaneous non-winged preovules such as *Elkinsia*, *Moresnetia* and *Archaeosperma*. The development of the sarcotesta in the preintegument lobes might significantly decrease the mass-to-area ratio, provided that the mass of the nucellus in *Warsteinia* was equivalent to that of other non-winged forms. As well as decreasing fall velocity, a winged morphology as shown could alternatively function by tumbling or saltation along the ground propelled by air movements (Ridley 1930) but the relative significance of either proposed dispersal optimizations is, of course, speculative. The reduction in fall velocity might be insignificant if the parent plant was of limited height of only one to several metres, as is presumed for slender early seed plants. The difficulty in assessing the real performance of winged diaspore structures among living forms, let alone fossils, is aptly demonstrated in studies of fruit dispersal in *Acer saccharinum*, in which it has been found that the preferential timing of abscission at higher rather than ambient wind velocities effects the release of disapores, and that the drag created by the attached winged fruit is an important factor in this mechanism (Greene and Johnson 1992).

The presence of winged seed diaspore structures by the late Devonian could be interpreted as an amelioration of a less derived preovule morphology with the possibility of, in one way or another, optimizing dispersal whether by influencing fall velocity, ground saltation, drag-related abscission or a combination of these. In terms of size, the preovules are consistent with the other contemporaneous Devonian and many Lower Carboniferous preovules. In a discussion of seed dispersal in the fossil record, Tiffney (1986) demonstrated that estimated volumes of Devonian preovules were approximately between 1 and 10 mm³. This range would include the nucellar region of *Warsteinia* if reconstructed as an ovoid three-dimensional structure.

Between the earliest records of seed plant preovules in the upper Famennian, characterized by open preintegument lobes, and the late Carboniferous trend towards an entire integument which has characterized all seed plants since, a wide variability of preovule preintegument forms existed among seed plants retaining hydrasperman reproduction. Attempts to explain the adaptive significance of the preintegument should focus on (1) the evolutionary *appearance* of a lobed preintegument and (2) the morphological diversification following the establishment of preovule organization in seed plants. In terms of an adaptive interpretation of the appearance of the preintegument, a general consensus appears to indicate no strong evidence for either a significantly protective rôle, which may have been carried out adequately by the megasporangial wall, as in other heterosporous groups, or for optimizing pollen capture. Either or both of these processes may have played important rôles later during the diversification of hydrasperman seed plants prior to entire integumentation. A selective pressure for optimizing food reserve availability has also been attributed to the preintegument in partitioning available food reserves and favouring the provisioning of pollinated/fertilized rather than unfertilized preovules (Westoby and Rice 1982; Haig and Westoby 1989). It is uncertain whether such a mechanism would have been functional among the earliest seed plants in which tissue differentiation of the preintegument lobes is simple and intimately associated with the nucellus only in the basal area. As with other possible functions of the preintegument, this could have been significant in more derived seed plant organizations where the preintegument was intimately fused with the nucellar tissue.

The interpretation proposed here is that the appearance of terete preintegument lobes could have been initially non-adaptive, but open to a range of possible mutational and developmental shifts in terms of fusion, tissue proliferation and changes in the amount and positioning of the vascular supply. The *de novo* evolution of the preintegument radically enlarged the potential for elaboration and fine-tuning of life history processes. The adaptive or non-adaptive nature of other 'key' elements of the seed habit include processes concerned with the apical opening of the nucellus and the lagenostome, pollen chamber, pollen chamber floor and central column mechanism attributed to plants with hydrasperman reproduction (Rothwell 1986). The evolution of the pollination

mechanism allowed early seed plants to jump the 'adaptive valley' separating water dependant, free-sporing heterospory from the seed habit (Chaloner and Pettitt 1987; Bateman and DiMichele 1994). Whether all the elements of the hydrasperman apparatus listed above appeared simultaneously or whether another configuration such as that observed in *Coumiasperma remyii* may have preceded it remains to be elucidated. Unlike the difficulty in assigning an unequivocal function to the preintegument, the pollination mechanism represented by a simple distal aperture is more easily interpreted as being spontaneously adaptive, even if initially less complex than the full suite of characters comprising hydrasperman reproduction outlined above.

The range of preintegument variations among hydrasperman seed plants prior to the development of the entire integument and integumental micropyle is striking, but, like the difficulties in interpreting the original appearance of the preintegument, the ecological and selective scenarios explaining this diversity have recently been hotly debated. This uncertainty is basically polarized into two general themes. Firstly, that the range of forms are representative of selective conditions characterized by a lack of biotic competition: an open selective landscape with a range of vacant niches (DiMichele *et al.* 1989). Another interpretation is that the range of variability observed among preovule types represents specialized adaptations fitted for specific niches and consequently consistent with conditions of biotic competition (e.g. Andrews 1963; Rothwell and Scheckler 1988).

Because of the shortage of palaeoecological information and whole plant reconstructions from many of these early seed plant assemblages, the range of niches available and/or exploited and the nature of any biotic and abiotic stresses are largely unknown. Furthermore, the morphology and organization of the preovule is, of course, only one of many characteristics contributing to that plant's overall fitness. Evidence from other studies indicates that by the late Tournaisian, hydrasperman seed plants probably comprised a relatively wide range of growth habits and physical niches from large self-supporting, arboreous trees, with small fronds and leaf abscission, to slender semi-self-supporting plants bearing large fronds (Gordon 1935; Long 1979; Galtier 1992; Rowe *et al.* 1993; Speck and Rowe 1994). Provisional reconstructions of several of these plants (Retallack and Dilcher 1988) indicate that all probably possessed hydrasperman preovules differing in preintegument and cupule morphology, but that all possessed the same type of hydrasperman pollination mechanism. It would be surprising, given the range of these growth forms by the end of the Tournaisian, if there was no biotic competition for niches among plants with a seed habit. There is no reason also why the increase in biotic competition characterizing the latter part of this scenario should be only between early pteridosperms and not between pteridosperms and other contemporaneous elements such as rhacophytosid ferns, as there is some palaeoecological evidence that the latter were in close succession ecologically and temporally to stands of early seed plants (Scheckler 1986; Rothwell and Scheckler 1988).

Another possible selective scenario is that the absence of a dormancy mechanism (Tiffney 1986; Mapes *et al.* 1989) and germination to specific environmental cues might have been an important constraint on the direction of life history strategies among early seed plants. If embryo development occurred continuously after fertilization, presumably while still attached to the parent sporophyte, there would have been a trade-off between the advantages of size increase and 'rigour' of the embryo against the increasing mass of the potential diaspore and its corresponding decrease in dispersal potential. The general absence of embryos preserved within preintegumented hydrasperman diaspores in the fossil record and the abundance of preserved pre-pollination stages has been discussed as evidence of an absence of dormancy among early hydraspermans prior to the earliest evidence of arrested development in a seed plant embryo in a Late Carboniferous cordaitan seed (Tiffney, 1986; Mapes *et al.* 1989). Coupled with unarrested embryo development is the dispersal potential of the earliest hydrasperman seeds, and the effects of mortality factors connected with density and distance in relation to the maternal plant or between siblings with regard to shading, pathogens, predators and competitors. Besides this, the absence of a dormancy mechanism and control of germination, during arguably the most vulnerable point in the seed plant life cycle, may indicate that the potential of the earliest hydrasperman seed plants to invade drier habitats might be overrated and that their reproductive success lies elsewhere, such as in the sheer output

of successfully fertilized diaspores. It is arguable whether the early stages of development of the hydrasperman seedling emerging from the preintegumented seed would have had more advantage in terms of size and presumed storage capability of metabolic reserves over early sporophyte growth stages implanted on exosporic gametophytes. Coupled with the constraints on development and dispersal outlined above, and linked with absence of dormancy, the size and likely nutrient storage properties of the earliest seeds could therefore be interpreted as another adaptive 'valley' in the transition towards a full seed habit superimposed on that concerned with pollen transfer and megasporangium/preovule shape. Establishment and emergence without a control of germination and dormancy, would represent an additional suite of constraints and possible adaptations among the earliest seed plants. The generally small size of the earliest seeds may therefore give some credence to the hypothesis of selective pressure for increased nutrient storage (Haig and Westoby 1989) possibly resulting from germination and development without dormancy control.

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REFERENCES

- ANDREWS, H. N. 1963. Early seed plants. *Science*, **142**, 925–931.
- ARBER, E. A. N. and GOODE, R. H. 1915. On some fossil plants from the Devonian rocks of North Devon. *Proceedings of the Cambridge Philosophical Society*, **18**, 89–104.
- ARTHUR, W. 1984. *Mechanisms of morphological evolution: a combined genetic, developmental and ecological approach*. John Wiley, New York, 275 pp.
- 1988. *A theory of the evolution of development*. John Wiley, New York, 94 pp.
- AUGSBURGER, C. K. 1986. Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees. *American Journal of Botany*, **73**, 353–363.
- BARNARD, P. D. W. and LONG, A. G. 1975. *Triradioxylon* – a new genus of Lower Carboniferous petrified stems and petioles together with a review of the classification of early pterophytina. *Transactions of the Royal Society of Edinburgh*, **69**, 231–250.
- BATEMAN, R. M. and DIMICHELE, W. A. 1994. Heterospory: the most iterative key innovation in the evolutionary history of the plant kingdom. *Biological Review*, **69**, 345–417.
- CALDER, M. G. 1938. On some undescribed species from the Lower Carboniferous flora of Berwickshire; together with a note on the genus *Stenomyelon* Kidston. *Transactions of the Royal Society of Edinburgh*, **59**, 309–331.
- CHALONER, W. G., HILL, A. J. and LACEY, W. S. 1977. First Devonian platyspermic seed and its implications in gymnosperm evolution. *Nature*, **265**, 233–235.
- and PETTITT, J. M. 1987. The inevitable seed. *Bulletin de la Société Botanique de France*, **134**, *Actualités Botaniques* 1987, **2**, 39–49.
- DIMICHELE, W. A., DAVIS, J. I. and OLMSTEAD, R. G. 1989. Origins of heterospory and the seed habit: the role of heterochrony. *Taxon*, **38**, 1–11.
- FAIRON-DEMARET, M. and SCHECKLER, S. E. 1987. Typification and redescription of *Moresnetia zaleskyi* Stockmans, 1948, an early seed plant from the Upper Famennian of Belgium. *Bulletin de l'Institut des Sciences Naturelles de Belgique, Sciences de la Terre*, **57**, 183–199.
- GALTIER, J. 1992. On the earliest arborescent gymnosperms. *Comptes Rendus de l'Académie des Sciences, Paris, Série II*, **314**, 1119–1125.
- and ROWE, N. P. 1989. A primitive seed-like structure and its implications for early gymnosperm evolution. *Nature*, **6230**, 225–227.
- 1991. A new permineralized seed-like structure from the basalmost Carboniferous of France. *Nouvelles Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **183**, 103–120.

- GILLESPIE, W. H., ROTHWELL, G. W. and SCHECKLER, S. E. 1981. The earliest seeds. *Nature*, **293**, 462–464.
- GORDON, W. T. 1935. The genus *Pitya*, Whitham, emend. *Transactions of the Royal Society of Edinburgh*, **58**, 279–311.
- GOULD, S. J. and VRBA, E. S. 1982. Exaptation – a missing term in the science of form. *Palaeobiology*, **8**, 4–15.
- GREEN, D. S. 1980. The terminal velocity and dispersal of spinning samaras. *American Journal of Botany*, **67**, 1218–1224.
- GREENE, D. F. and JOHNSON, E. A. 1992. Fruit abscission in *Acer saccharinum* with reference to seed dispersal. *Canadian Journal of Botany*, **70**, 2277–2283.
- HAIG, D. and WESTOBY, M. 1989. Selective forces in the emergence of the seed habit. *Biological Journal of the Linnean Society*, **38**, 215–238.
- HIGGS, K. and STREEL, M. 1984. Spore stratigraphy at the Devonian–Carboniferous boundary in the northern 'Rheinisches Schiefergebirge', Germany. *Courier Forschungsinstitut Senckenberg*, **67**, 157–179.
- KEUPP, H. and KOMPA, R. 1984. Mikrofazielle und Sedimentologische Untersuchungen an Devon/Karbon Profilen am Nordrand des Rechtsrheinischen Schiefergebirges. *Courier Forschungsinstitut Senckenberg*, **67**, 139–142.
- LONG, A. G. 1959. On the structure of *Calymmatotheca kidstoni* Calder (emended) and *Genomosperma latens* gen. et sp. nov. from the Calciferous Sandstone Series of Berwickshire. *Transactions of the Royal Society of Edinburgh*, **64**, 29–44.
- 1960a. On the structure of *Samaropsis scotica* Calder (emended) and *Euryostoma angulare* gen. et sp. nov., petrified seeds from the Calciferous Sandstone Series of Berwickshire. *Transactions of the Royal Society of Edinburgh*, **64**, 261–280.
- 1960b. *Stannosoma huttonense* gen. et sp. nov. – a pteridosperm seed and cupule from the Calciferous Sandstone Series of Berwickshire. *Transactions of the Royal Society of Edinburgh*, **64**, 201–215.
- 1961. Some pteridosperm seeds from the Calciferous Sandstone Series of Berwickshire. *Transactions of the Royal Society of Edinburgh*, **64**, 401–419.
- 1969. *Euryostoma trigona* sp. nov., a pteridosperm ovule borne on a frond of *Alcicornopteris* Kidston. *Transactions of the Royal Society of Edinburgh*, **68**, 171–182.
- 1975. Further observations on some Lower Carboniferous seeds and cupules. *Transactions of the Royal Society of Edinburgh*, **69**, 267–293.
- 1977a. Some Lower Carboniferous pteridosperm cupules bearing ovules and microsporangia. *Transactions of the Royal Society of Edinburgh*, **70**, 1–11.
- 1977b. Lower Carboniferous pteridosperm cupules and the origin of angiosperms. *Transactions of the Royal Society of Edinburgh*, **70**, 13–35.
- 1979. Observations on the Lower Carboniferous genus *Pitys* Witham. *Transactions of the Royal Society of Edinburgh*, **70**, 111–127.
- LUPPOLD, F. W., CLAUSEN, C. D., KORN, D. and STOPPEL, D. 1994. Devon/Karbon-Grenzprofil im Bereich von Remscheid-Altenaer Sattel, Warsteiner Sattel, Briloner Sattel und Attendorn-Elisper Doppelmulde (Rheinisches Schiefergebirge). 7–70. In KORN, D., CLAUSEN, C. D. and LUPPOLD, F. W. (eds). *Die Devon/Karbon-Grenze im Rheinschen Schiefergebirge*. Landschaftsverband Westfalen-Lippe, Münster, 221 pp.
- MAPES, G., ROTHWELL, G. W. and HAWORTH, M. T. 1989. Evolution of seed dormancy. *Nature*, **337**, 645–646.
- MATTEN, L. C. and LACEY, W. S. 1981. Cupule organization in early seed plants. 221–234. In ROMANS, R. C. (ed.). *Geobotany II*. Plenum, New York.
- and LUCAS, R. C. 1980a. Studies on the cupulate genus *Hydrasperma* Long from Berwickshire and East Lothian in Scotland and County Kerry in Ireland. *Botanical Journal of the Linnean Society*, **81**, 249–273.
- MAY, B. I. and LUCAS, R. C. 1980b. A megafossil flora from the Uppermost Devonian near Ballyheigue, Co. Kerry, Ireland. *Review of Palaeobotany and Palynology*, **29**, 241–251.
- TANNER, W. R. and LACEY, W. S. 1984. Additions to the silicified Upper Devonian/Lower Carboniferous flora from Ballyheigue, Ireland. *Review of Palaeobotany and Palynology*, **43**, 303–320.
- NIKLAS, K. 1981a. Simulated wind pollination and airflow around ovules of some early seed plants. *Science*, **211**, 275–277.
- 1981b. Airflow patterns around some early seed plant ovules and cupules: implications concerning efficiency in wind pollination. *American Journal of Botany*, **68**, 635–650.
- 1983a. Early seed plant wind pollination studies: a reply. *Taxon*, **32**, 99–100.
- 1983b. The influence of Paleozoic ovule and cupule morphologies on wind pollination. *Evolution*, **37**, 968–986.

- 1985. The aerodynamics of wind pollination. *The Botanical Review*, **51**, 328–386.
- 1992. *Plant biomechanics: an engineering approach to plant form and function*. University of Chicago Press, Chicago, 607 pp.
- PETTITT, J. M. and BECK, C. B. 1968. *Archaeosperma arnoldii* – a cupulate seed from the Upper Devonian of North America. *Contributions to the Museum of Paleontology, University of Michigan, Ann Arbor*, **22**, 139–154.
- PIJL, L. van der 1969. *Principles of dispersal in higher plants*. Springer Verlag, Berlin, 153 pp.
- RETALLACK, G. J. and DILCHER, D. L. 1988. Reconstructions of selected seed ferns. *Annals of the Missouri Botanical Gardens*, **75**, 1010–1057.
- RIDLEY, H. N. 1930. *The dispersal of plants throughout the world*. L. Reeve and Co., Ashford, 744 pp.
- ROGERS, I. 1926. On the discovery of fossil fishes and plants in the Devonian rocks of North Devon. *Transactions of the Devonshire Association for the Advancement of Science, Literature and Art*, **58**, 223–234.
- ROTHWELL, G. W. 1986 Classifying the earliest gymnosperms. 137–161. In SPICER, R. A. and THOMAS, B. A. (eds). *Systematic and taxonomic approaches in palaeobotany*. Oxford University Press, Oxford, 321 pp.
- and SCHECKLER, S. E. 1988. Biology of ancestral gymnosperms. 85–134. In BECK, C. B. (ed.). *Origin and evolution of gymnosperms*. Columbia University Press, New York, 504 pp.
- and GILLESPIE, W. H. 1989. *Elkinsia* gen. nov., a Late Devonian gymnosperm with cupulate ovules. *Botanical Gazette*, **150**, 170–189.
- and SERBET, R. 1992. Pollination biology of *Elkinsia polymorpha*, implications for the origin of gymnosperms. *Courier Forschungsinstitut Senckenberg*, **147**, 225–231.
- 1994. Lignophyte phylogeny and the evolution of spermatophytes: a numerical cladistic analysis. *Systematic Botany*, **19**, 443–482.
- and WIGHT, D. C. 1989. *Pullaritheca longii* gen. nov. and *Kerryia mattenii* gen. et sp. nov., Lower Carboniferous cupules with ovules of the *Hydrasperma tenuis*-type. *Review of Palaeobotany and Palynology*, **60**, 295–309.
- ROWE, N. P. 1992a. Winged Late Devonian seeds. *Nature*, **359**, 682.
- 1992b. Permineralized Tournaisian plants from Oberrödinghausen in the 'Rheinisches Schiefergebirge', Germany. *Conrrier Forschungsinstitut Senckenberg*, **147**, 127–135.
- and GALTIER, J. 1990. A Lower Carboniferous plant assemblage from La Serre (Montagne Noire, France). Part II. Gymnosperms. *Review of Palaeobotany and Palynology*, **63**, 91–115.
- SPECK, T. and GALTIER, J. 1993. Biomechanical analysis of a Palaeozoic gymnosperm stem. *Proceedings of the Royal Society of London*, **252**, 19–28.
- SCHECKLER, S. E. 1986. Geology, floristics and paleoecology of Late Devonian coal swamps from Appalachian Laurentia (U.S.A.). *Annales de la Société Géologique Belgique*, **109**, 209–236.
- SPECK, T. and ROWE, N. P. 1994 Biomechanical analysis of *Pinus dayi*: early seed plant vegetative morphology and its implications on growth habit. *Journal of Plant Research*, **107**, 443–460.
- STEWART, W. N. 1983. *Paleobotany and the evolution of plants*. Cambridge University Press, Cambridge, 405 pp.
- STOCKMANS, F. 1948. Végétaux du Dévonien supérieur de la Belgique. *Mémoires du Musée Royal d'Histoire Natuelle de Belgique*, **110**, 1–85.
- TIFFNEY, B. H. 1986. Evolution of seed dispersal syndromes according to the fossil record. 273–305. In MURRAY, D. R. (ed.). *Seed dispersal*. Academic Press, Sydney, Australia. 322 pp.
- WESTOBY, M. and RICE, B. 1982. Evolution of seed plants and inclusive fitness of plant tissues. *Evolution*, **36**, 713–724.

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